Avian prey of the Australian Ghost Bat *Macroderma gigas* (Microchiroptera: Megadermatidae): prey characteristics and damage from predation

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ABSTRACT

The Ghost Bat *Macroderma gigas* is a large (mean mass 150 g) predatory bat of subtropical and tropical Australia. It carries its vertebrate prey to roost caves to be eaten and where remains are dropped and accumulate. Whereas the attack and feeding methods of *M. gigas* on mammals has been well documented, there is little comparable information relating to avian prey. Using published lists of avian prey and skeletal material collected from a modern *Macroderma* roost, this study examined the range of bird species eaten by this bat. From the characteristics of these birds, biases towards particular behaviour patterns were identified. Prey masses were used to determine a preferred size range for avian prey. From this information, and assessments of the damage to the bones, inferences were made regarding the capture and processing methods employed by *M. gigas* for birds. More than 50 species, from a broad taxonomic range, have been recorded as avian prey of the Ghost Bat. These are all essentially diurnal with the obvious exception of the Australian Owlet-nightjar *Aegotheles cristatus*. Species that aggregate when roosting are over-represented in the diet of the Ghost Bat. Ground-frequenting species comprise about a quarter of the prey records. Birds may be captured at most levels of the strata, from the ground to the canopy, and in flight. Ghost Bats feed on a wide size range of avian prey, and although they may take animals up to about two-thirds their own mass, they have a preference for smaller birds, with almost 70% of the species having a mass less than 35 g. The most severe damage to a bird's post-cranial skeleton is to the ventral side of the sternum, whereas distal appendicular elements exhibit no damage from Ghost Bat predation. The type of damage to the bones and the size of the prey is consistent with the assumption that megadermatid bats were accumulators of many avian remains now represented in Miocene and Pliocene fossil deposits at Riversleigh, Queensland.

Key words: Ghost Bat, Bat edict, Avian prey, Fossil bat prey, *Macroderma gigas*.

INTRODUCTION

The Ghost Bat *Macroderma gigas* is a large (up to 165 g; mean 150 g) predatory bat of subtropical and tropical Australia (Richards and Hand 1995) (Fig. 1). It feeds on both vertebrate and invertebrate prey, which are carried back to roost caves to be eaten, and where their remains are dropped to the cave floor. Eventually discarded portions accumulate, providing an indication of the prey species of the Ghost Bat. Although *M. gigas* is the only species of megadermatid now occurring in Australia, eight Australian fossil species have been recorded (Hand 1985, 1995, 1996; Hand *et al.* 1988). These have been implicated as the source of the accumulations of some of the deposits of small vertebrates discovered in the Tertiary fossil deposits of Riversleigh, northwestern Queensland (Boles 1995, 1997, 1998; Hand 1990, 1995, 1996).

Published work on *M. gigas* has included lists of prey species identified from active roosts (Douglas 1967; Vestjens and Hall 1977; Pettigrew *et al.* 1985; Toop 1985; Schulz 1986) and studies of foraging methods, including attack methods on mammals, by this species (Guppy and Coles 1983; Kulzer *et al.* 1984; Tidemann *et al.* 1985). Ghost Bats emerge from their roosts and commence hunting about 1 to 1.5 hours after sunset for a period of two hours. This is followed by periods of inactivity, punctuated by short bursts of foraging. Resumption of feeding activity takes place in the early morning, up to just before sunrise (summarized from Tidemann *et al.* 1985). The initial foraging behaviour of *M. gigas* has been characterized as "sit and inspect", in which bats quietly visually inspect their surroundings for movement from a perch (Tidemann *et al.* 1985). Apparently they are unable to detect motionless animals. Once prey is located, it may be captured in the air, gleaned (taken from the surface of the substrate by a flying bat) from the ground or foliage, or dropped on from a perch. The bats are dependent on stealth and darkness to capture prey. Toop (1985) noted that a bird in an illuminated room was able to elude capture.

Using mice as prey under captive conditions, Kulzer *et al.* (1984) reported that an attack flight by *M. gigas* culminated when the bat dropped on its prey, enclosing it with the wings and immediately biting it on the

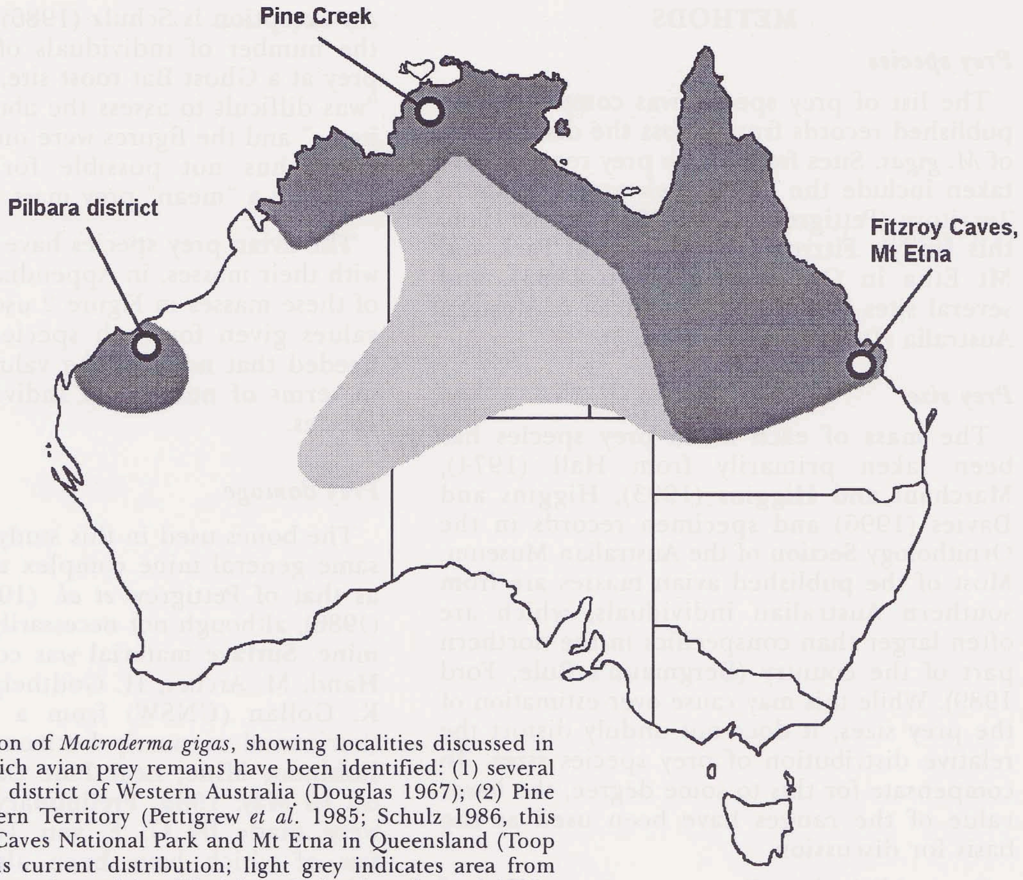

Figure 1. Distribution of *Macroderma gigas*, showing localities discussed in this paper from which avian prey remains have been identified: (1) several sites in the Pilbara district of Western Australia (Douglas 1967); (2) Pine Creek area, Northern Territory (Pettigrew *et al.* 1985; Schulz 1986, this study); (3) Fitzroy Caves National Park and Mt Etna in Queensland (Toop 1985). Dark grey is current distribution; light grey indicates area from which species is now extirpated (modified from Richards and Hand 1995).

head, neck or throat. If this did not result in immediate death, the prey was positioned for additional bites to the head. Prey up to 60 g was carried to the roost with the head in the bat's jaws. Consumption commenced with the skull. Smaller mice (*c.* 10 g) were completely eaten, whereas parts of adults (remnants of skull, legs, digestive tract and tail) were sometimes dropped to the floor. Guppy and Coles (1983) gave similar descriptions of the feeding behaviour of captive *M. gigas*. Douglas (1967) noted that the bats ate the whole carcass of mammalian prey, including the fur, although portions were often dropped.

In contrast to several studies that have been conducted on mammalian prey, there is little information on how *M. gigas* attack or process birds as prey. Pettigrew *et al.* (1985) observed a *M. gigas* unsuccessfully pursue a flying quail *Coturnix* (presumably Brown Quail *C. ypsilophora*). Douglas (1967) noted that in captivity the bats grasped dead birds across the chest and recorded that when they ate birds, "the feathers were discarded where possible and wing and tail quills, and the legs, were dropped to the ground". There do not appear to be any other descriptions of the methods of attacking, killing or transporting avian prey. Published identifications of avian prey of *M. gigas* have been made almost exclusively on discarded heads and feathers; as yet no author has indicated that identifications were based on bones. To date, no attention has been focused on the manner of feeding on and resultant damage by this predatory bat species to avian prey.

Thus, using avian skeletal material collected from a modern *M. gigas* roost, the type of damage to the bones is described in this study. This information is used for indications of the attack and processing methods that the bats use on avian prey, particularly in comparison with published information on mammalian prey. From published lists of prey and the remains included in this study, characteristics of prey species are reviewed for any biases towards particular taxonomic groups, or foraging or other behavioural patterns. Avian predators, such as owls, that serve as accumulators, can often be identified to species based on the size range of the prey. Using the lists of prey, the size range of the avian prey of *M. gigas* is assessed. These results are also evaluated for consistency with the idea that Miocene and Pliocene *Macroderma* were responsible for the accumulations of some of the avian remains found as fossils at Riversleigh.

METHODS

Prey species

The list of prey species was compiled from published records from across the distribution of *M. gigas*. Sites from which prey records were taken include the Pine Creek area, Northern Territory (Pettigrew *et al.* 1985; Schulz 1986, this study), Fitzroy Caves National Park and Mt Etna in Queensland (Toop 1985), and several sites in the Pilbara district of Western Australia (Douglas 1967) (Fig. 1).

Prey size

The mass of each avian prey species has been taken primarily from Hall (1974), Marchant and Higgins (1993), Higgins and Davies (1996) and specimen records in the Ornithology Section of the Australian Museum. Most of the published avian masses are from southern Australian individuals, which are often larger than conspecifics in the northern part of the country (Bergmann's Rule; Ford 1989). While this may cause over-estimation of the prey sizes, it does not unduly distort the relative distribution of prey species sizes. To compensate for this to some degree, the lower value of the ranges have been used as the basis for discussion.

Few published studies report the number of each prey species present; most merely indicate the presence of a species in prey remains. An exception is Schulz (1986), who estimated the number of individuals of each taxon of prey at a Ghost Bat roost site, warning that it "was difficult to assess the abundance of prey items" and the figures were only approximate. It is thus not possible for this study to calculate a "mean" prey mass.

The avian prey species have been tabulated, with their masses, in Appendix 1. A histogram of these masses in Figure 2 uses the minimum values given for each species. It should be heeded that none of the values is quantified in terms of number of individuals per prey species.

Prey damage

The bones used in this study come from the same general mine complex near Pine Creek as that of Pettigrew *et al.* (1985) and Schulz (1986), although not necessarily from the same mine. Surface material was collected by S. J. Hand, M. Archer, H. Godthelp, K. Aplin and K. Gollan (UNSW) from a series of adits (horizontal or nearly horizontal passages) in Kohinoor Mine, near Pine Creek, conducted on 10 May, 1983. Preliminary identifications were made by G. F. van Tets (CSIRO), a few of which have been altered following subsequent examination by the author. The prey species and skeletal elements recorded are given in Appendix 2.

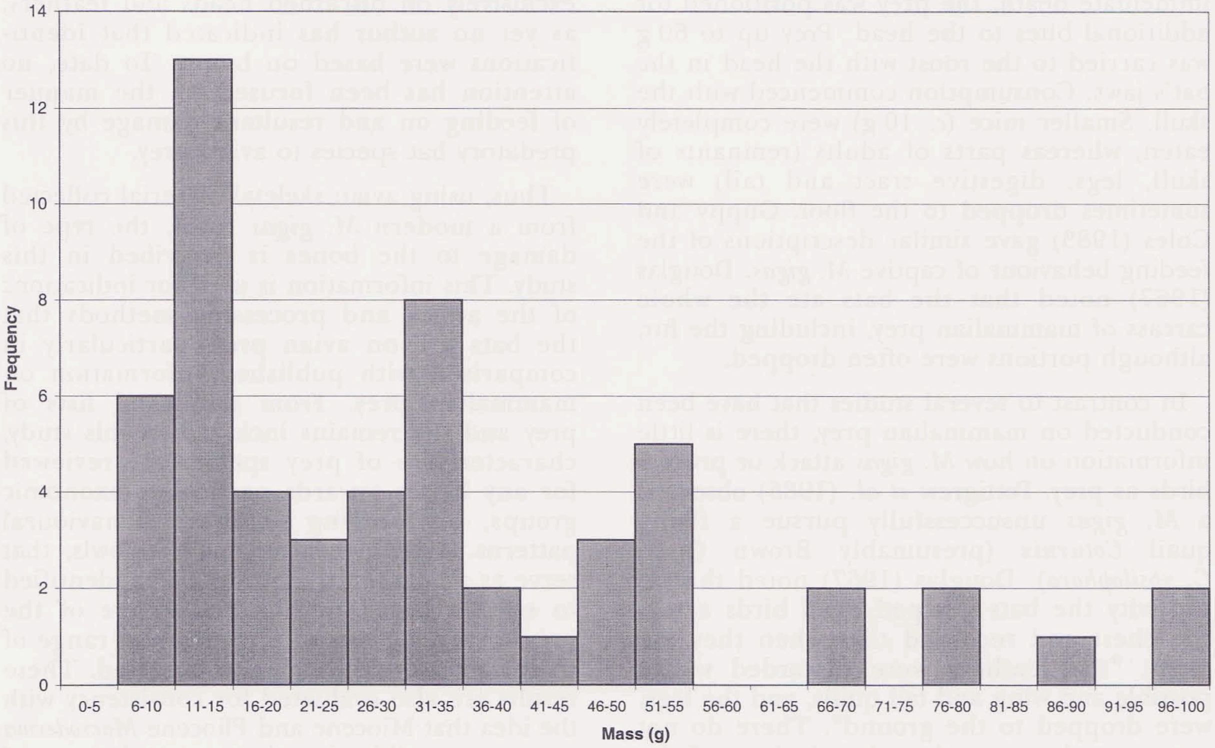

Figure 2. Histogram showing range and frequencies of minimum avian prey masses (g) taken from Appendix 1. The indeterminate crake *Porzana* has been omitted because of the considerable difference in mass between the two species that might be represented.

RESULTS

Prey species

Over 50 species of birds have been identified as prey of *M. gigas* (Appendix 1). Twenty-two species were recorded from Mt Etna by Toop (1985), (although he named only three of these). This compares with 21 species identified from the Pilbara (Douglas 1967) and 40 from Pine Creek (Pettigrew *et al.* 1985; Schulz 1986, this study). Only one species, the Australian Owlet-nightjar *Aegotheles cristatus*, was recorded from all three localities. A few species were found in both the Northern Territory and Western Australian roosts. Most species were represented at only one site.

These encompass a broad taxonomic range, but with songbirds (Passeriformes) dominating, comprising about two-thirds of the species. Most major bird groups are represented with the exceptions of waterbirds (other than crakes), raptorial birds and those containing only very large-bodied forms. All species were essentially diurnal with the exception of *Aegotheles cristatus*. A substantial number of the prey species are ground-frequenting (n = 19) or aggregate when roosting (n = 15).

Among the avian remains examined in this study were several that represented young birds, as indicated by the pitted surface of the bone and incomplete ossification of the articular facets (for example, cf. Silver-crowned Friarbird *Philemon argenticeps*; Appendix 2; Fig. 3H).

Prey size

Throughout the distribution of *M. gigas*, prey species in the size range of 6–40 g predominate, but in the Northern Territory population this upper boundary extends to 50–60 g. Very few heavier birds (>70 g) have been recorded. These assessments are based on the species list without allowance for the numbers of individuals in each size class. Schulz's (1986) rough estimates indicated that within this broad size range there was a bias towards the smaller end of the scale, with about a third of the prey items falling in the 10–20 g class. Of the prey species in Appendix 1, almost 70% have a mass of 35 g or less (Fig. 2).

Prey damage (Fig. 3)

Skull

Only one avian skull was examined. It showed minor damage to the rear, which may not have resulted from *M. gigas* predation. There was no injury of the magnitude described for the consumption of mice. A bill of a kingfisher exhibits breakage that appears to be unrelated to predation by *M. gigas*. Douglas (1967) identified some avian prey from heads found in roosting caves, but did not indicate what sort of damage these had incurred.

Pectoral girdle

Several coracoids were recovered intact. On one badly damaged sternum the posterior ends only of the coracoids were still in contact and the shafts showed marked laceration (Fig. 3A). In two other instances the sterna were badly chewed but the still attached coracoids were undamaged (Fig. 3D). A scapula had minor damage to its posterior tip, which may have been the result of chewing by *M. gigas*.

Sternum

All the four sterna examined had sustained severe damage (Fig. 3A-D). The keels were heavily lacerated along their ventral margins, showing extensive evidence of chewing, and in several instances this extended through the entire depth of the keel to the sternal plate. The damage also occurred along at least one of lateral sides of the sternum. In some instances the sternal plate had been removed almost to the base of the keel. The posterior portion of the sternum was missing in all instances.

Synsacrum

No complete pelvic elements were found. In one specimen, the anterior end of the ilium appeared to have been chewed to about the acetabulum; the ischium and pubis showed no such damage (Fig. 3G). The anterior vertebrae of the synsacrum (thoracic, lumbar) were not recovered. Two sets of sacral vertebrae were detached from the pelvic elements and appeared to have been chewed on the anterior end and for part of the lateral edge on one side (Fig. 3E-F).

Wing and leg

Distal elements of wings (ulna, radius, carpometacarpus, digits) and legs (tibiotarsus, tarsometatarsus) exhibited no indication of damage from *M. gigas*. No humeri were recovered except for an instance in which the wing, sternum and coracoids remained joined. In this case, most of the humerus was missing, with only the extreme proximal and distal ends being present, held together and attached to the remaining bones by dried tissue (Fig. 3B). The loss of the shaft may have resulted from chewing. The only femur recovered was a distal-most fragment; the slight damage to it did not appear to be due to *M. gigas*.

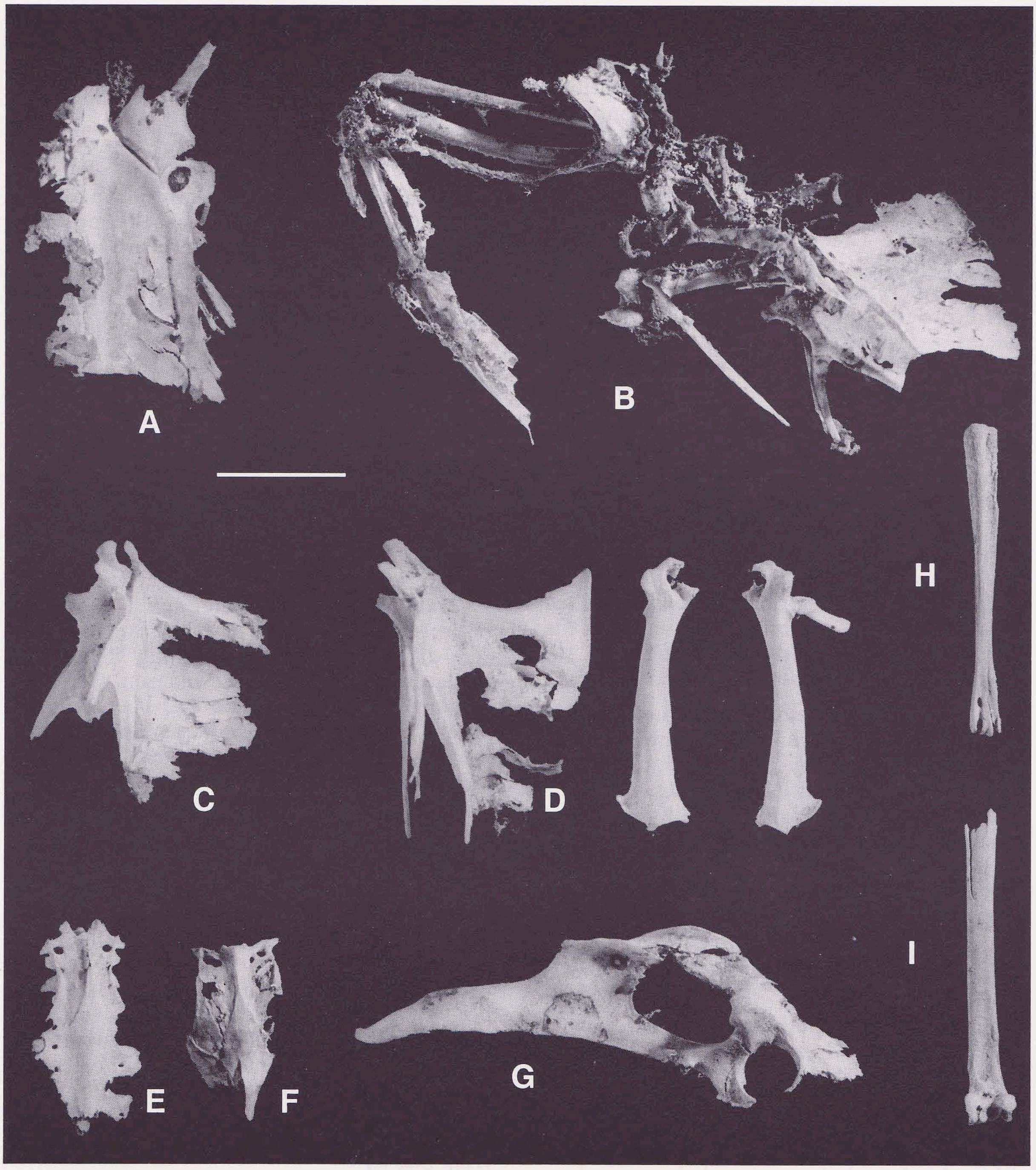

Figure 3. Avian bones from Kohinoor Mine, Northern Territory, damaged by Ghost Bats. A. Sternum of *Trichoglossus haematodus* with remnant of coracoid. B. Sternum, pectoral girdle and forelimb of *Geopelia cuneata*, showing proximal fragment of humerus. C. Sternum of *Geopelia striata*. D. Sternum of *Turnix castanota* with undamaged coracoids. E. Synsacrum of *Geopelia striata*. F. Synsacrum of *Trichoglossus haematodus*. G. Pelvic fragment of *Geopelia cuneata*. H. Tibiotarsus of large honeyeater (cf. *Philemon argenticeps*) showing porous surface and incompletely formed articular surfaces, indicative of immaturity. I. Tibiotarsus of *Philemon argenticeps* exhibiting post-mortem damage to shaft not resulting from Ghost Bat predation. Bar equals 10 mm for all figures except G, for which it equals 5 mm.

DISCUSSION

Prey species

Based on the list of recorded avian prey, *M. gigas* appears to select its prey opportunistically. Among the wide range of taxonomic groups, the only ones that are over-represented are those with species that tend to aggregate when roosting. The most obvious of these are the four species of woodswallows *Artamus*. Individuals often roost in close proximity, a habit that presumably makes them more easily located. Other social species that roost in close aggregations include the lorikeets *Trichoglossus* and *Psitteuteles*, Budgerigar *Melopsittacus undulatus*, Rainbow Bee-eater *Merops ornatus*, Varied Sittella *Daphoenositta chrysoptera* and finches *Taeniopygia, Poephila, Erythura* and *Emblema*. These are indicated in Appendix 1 and Figure 2. Individuals of the Grey-crowned Babbler *Pomatostomus temporalis* roost in close association but within an enclosed shelter.

The nocturnal Australian Owlet-nightjar *Aegotheles cristatus* is the obvious exception among the otherwise primarily diurnal avian prey species. It emerges and becomes active at the same time as *M. gigas*. Because it could be captured not only when perched, but also in flight or on the ground when feeding, it is not surprising that this species was recorded by four studies. Other species, such as quail *Coturnix*, button-quail *Turnix* and crakes *Porzana*, are frequently active at night, and a number of species vocalize on moonlit nights; both these behaviours would increase the risk of predation by *M. gigas*. Most diurnal birds will have gone to their roosts for the night before the bats emerge, but may not have completely settled. Any movement would make them potentially detectable to the bats. Many species begin vocalizing and becoming active before sunrise, corresponding with the early morning foraging bout of the bats, again making them vulnerable to detection and attack.

At a central coastal Queensland colony, Toop (1985) noted that ground-dwelling prey were rarely taken, and contrasted this with the practice of *M. gigas* in desert habitats. The three species named of the 22 he recorded were arboreal. The lists of prey species from drier country colonies of *M. gigas* of the Northern Territory and Western Australia confirm that a substantial proportion is ground-frequenting. A somewhat arbitrary delimitation of ground-frequenting species comprises those that feed and nest on the ground (quail *Coturnix*, button-quail *Turnix*, crake *Porzana*, Spinifex Pigeon *Geophaps plumifera*, Chestnut-breasted Quail-thrush *Cinclosoma castaneothorax*, Rufous Songlark *Cincloramphus mathewsi*, Richard's Pipit *Anthus novaeseelandiae*) and those feed extensively on the ground but roost and nest in trees or shrubs (doves *Geopelia*, Red-backed Fairy-wren *Malurus melanocephalus*, Striated Grasswren *Amytornis striatus*, Grey-crowned Babbler *Pomatostomus* and finches *Taeniopygia, Poephila, Erythura* and *Emblema*). These groups are designated in Appendix 1 and Figure 2. Seven of the species made up about one-third of the individual avian remains from 29 species identified by Schulz (1986). Likewise nine of the 40 species recorded by Douglas (1967) fall into these categories.

That these species are largely ground-frequenting does not necessarily mean that they were captured on the ground (note observation by Pettigrew *et al.* (1985) of the attempted capture of a flying quail). Many of the birds that nest and forage on the ground roost above it, as do almost all of the other recorded prey species. The range of avian prey species indicates *M. gigas* will capture birds at almost any level, from the ground or elevated perches, and in flight.

It is known that inexperienced young birds have a higher mortality from predators than do older individuals (Newton 1993; Sullivan and Roper 1996), and it is likely that young birds form a significant proportion of the prey of *M. gigas*. They would be more easily captured and possibly less skilled in defending themselves, thus reducing potential injury to the bat. This could be particularly important with larger birds with strong bills and claws, such as the young Pied Butcherbird *Cracticus nigrogularis* recorded by Schulz (1986). Old or weak birds might also be expected to form a disproportionate amount of the prey; however, these are features that cannot be assessed from examination of the remains.

The list of prey species shows differences between the colonies of *M. gigas*, as well as occurrences common to two or all colonies (Appendix 1). In some cases, a widespread bird species that occurs throughout the distribution of *M. gigas* has been recorded as prey from only one location (e.g., *Merops ornatus*). This is likely to be an artefact of the small number of samples. Other prey species live in only part of the predator's range. The few records from the Mt Etna colonies in Queensland include several rainforest species (e.g., *Meliphaga lewinii, Colluricincla megarhyncha*), whereas among the avian prey of the Pilbara colonies are desert species (e.g., *Amytornis striatus, Cinclosoma castaneothorax*). There are insufficient published records from the coastal eastern colony to make further comparisons.

Prey size

The records compiled here indicate that *M. gigas* will take a range of avian prey sizes but generally selects smaller species, with a third of those recorded falling below 20 g and more than two-thirds less than 35 g. The extent to which this choice of prey species is actually based on size, rather than factors such as opportunism, prey detectability and roosting habits cannot be determined. The records of large prey species (>80 g) in the wild, although few, are interesting. If the individual birds captured were towards the high end of their mass range, it would mean that the bats were taking prey about two-thirds their own mass. As well as the increased difficulty of killing such large prey, the chance of injury is increased and ability to return these to the roost for consumption is compromised. Kulzer *et al.* (1984) reported that captive bats would kill and transport rats up to 80% of their body mass. This may be an artefact of the sizes of food animals offered and probably should be extrapolated to wild situations with care. The record of a Pied Butcherbird *Cracticus nigrogularis*, a species that as an adult would both be heavy and offer the most risk of injury, refers to a young bird (Schulz 1986), which would not present these problems to the same degree. Kulzer *et al.* (1984) noted that captive *M. gigas* were able to kill 100 g young rats without sustaining any injury.

Prey damage

It is not evident from the remains what attack methods are employed by *M. gigas* on birds; however, there is no reason to believe that a novel technique is used relative to those observed with non-avian prey. The patterns of damage to the post-cranial bones of avian prey are consistent with the general observations by Kulzer *et al.* (1984) that mice are consumed along the anteroposterior midline of the body. At the same time, remains of sterna suggest that *M. gigas* feeds on birds in a manner somewhat different from that used for mammals. In contrast to observations on mice used in feeding experiments (Douglas 1967; Guppy and Coles 1983; Kulzer *et al.* 1984), birds are not eaten whole. That the major damage is to the keel and lateral edges of the sternum, while the coracoids frequently escape any damage, suggests that the principal portion of a carcass consumed is on the ventral side of the bird, presumably the pectoral muscle. The loss of the posterior end of the sterna in all four of the remains that were examined suggests that entry may also be made into the body cavity.

There was no evidence available to assess whether the skull of birds sustained the same damage as did those of mice in experiments. If feeding by the bats had commenced at the skull and continued posteriorly, as described by Kulzer *et al.* (1984) for mice, then the coracoids would be expected to sustain more damage than was observed.

The absence of damage to distal appendicular elements is consistent with observations that these portions are discarded by the bat before feeding. Identifications of avian prey by previous authors have been based largely on feathers, without indicating which feathers were used. It is probable that most of the latter records were based on the large feathers of the wing (remiges) and tail (rectrices), which Douglas (1967) noted are dropped by feeding birds. These feathers are generally the most easily noticed and collected, and usually among the easiest to identify. The remiges are connected to the bones of the hand, and so would remain attached to the discarded wings.

The small sample of modern bones collected in this study agrees with the pattern of small avian bones recovered at Riversleigh (Boles 1995, 1997, 1998). At Riversleigh, there were ample distal elements (carpometacarpi, tibiotarsi, tarsometatarsi) in the fossil deposits. These were often broken but the damage appears to be post-depositional. Coracoids, although much fewer than distal long bones, exceed proximal long bones. Humeri and femora from small-bodied forms are unusual. Skulls, sterna and pelvic elements are even less commonly found, no doubt due to their comparative fragility compared to the long bones.

Conclusions in relation to Riversleigh remains

Examination of avian prey remains from modern Ghost Bat colonies has shown that the skeletal elements represented and the manner of damage these have sustained from *M. gigas* predation are consistent with findings on avian fossils from Riversleigh. This supports the assumption that megadermatid bats were accumulators of avian remains in these deposits. Owls are well documented as accumulators of vertebrate remains in caves in Australia and elsewhere (Baird 1991). To date, however, no evidence of owls has been recovered from the Riversleigh deposits.

There is also strong concordance between the size of the prey animals from the fossil sites and modern Ghost Bat caves. This agreement extends to the few taxa that have thus far been identified from the Riversleigh megadermatid accumulations. Taxa that have been recognized include a small kingfisher (Boles 1997), Budgerigar *Melopsittacus undulatus* (Boles 1998), and a swallow and honeyeaters (unpublished data).

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APPENDIX 1

Recorded avian prey species of the Ghost Bat *Macroderma gigas*, giving body masses (see text for sources) and references to localities for species' occurrence as prey. (1) Pilbara, Western Australia (Douglas 1967); (2) Pine Creek, Northern Territory (Pettigrew *et al.* 1985); (3) Pine Creek, Northern Territory (Schulz 1986); (4) Pine Creek, Northern Territory (this study); (5) Mt Etna, Queensland (Toop 1985). ** — feeds and nests on the ground; * — feeds but not nests on the ground'; **A** — aggregates when roosting.

Scientific Name	English Name	Mass (g)	WA	NT	Qld
** +*Coturnix ?ypsilophora*	Brown? Quail	90–120		2	
** *Porzana pusilla/tabuensis*	Baillon's/Spotless Crake	14–42/ 39–58		4	
** *Turnix maculosa*	Red-backed Button-quail	31–48		3	
** *Turnix velox*	Little Button-quail	33–55	1		
** *Turnix castanota*	Chestnut-backed Button-quail	69–87		4	
* *Geopelia striata*	Peaceful Dove	44–52		2,3	
* *Geopelia cuneata*	Diamond Dove	32–36	1	2,3,4	
** *Geophaps plumifera*	Spinifex Pigeon	80–106	1		
A *Trichoglossus haematodus*	Rainbow Lorikeet	80–124		4	
A *Psitteuteles versicolor*	Varied Lorikeet	51–62		3,4	
Psephotus dissimilis	Hooded Parrot	54–56		2,3	
A *Melopsittacus undulatus*	Budgerigar	20–31	1		
Aegotheles cristatus	Australian Owlet-nightjar	34–49	1	2,3	5
Apus pacificus	Fork-tailed Swift	38–54		4	
Alcedo azureus	Azure Kingfisher	26–37		4	
Todiramphus sp. [*sanctus/pyrrhopygia*]	kingfisher	30–45/ 47–57	1	2,4	
Todiramphus ?macleayii	Forest? Kingfisher	30–43		4	
Todiramphus pyrrhopygia	Red-backed Kingfisher	47–57		3	
A *Merops ornatus*	Rainbow Bee-eater	24–33		3	
Eurystomus orientalis	Dollarbird	98–120		3	
Climacteris melanura	Black-tailed Treecreeper	30–41	1		
Pardalotus striatus	Striated Pardalote	7–10		3	
Gergyone olivacea	White-throated Gerygone	6–9		3	
* *Malurus melanocephalus*	Red-backed Fairy-wren	6–8		2	
* *Amytornis striatus*	Striated Grasswren	15–23	1		
Philemon argenticeps	Silver-crowned Friarbird	68–100		4	
Philemon citreogularis	Little Friarbird	55–70		3	
Manorina flavigula	Yellow-throated Miner	48–58		3	
Meliphaga lewinii	Lewin's Honeyeater	30–38			5
Lichenostomus virescens	Singing Honeyeater	20–28	1		
Lichenostomus keartlandi	Grey-headed Honeyeater	13–15	1	3	
Lichenostomus penicillatus	White-plumed Honeyeater	14–18	1		
Lichenostomus flavescens	Yellow-tinted Honeyeater	11–15		3	
Lichmera indistincta	Brown Honeyeater	10–12		2,3	
Melanodryas cucullata	Hooded Robin	20–25	1		
Microeca fascinans	Jacky Winter	11–13		3	
A *Daphoenositta chrysoptera*	Varied Sittella	10–14		3	
Pachycephala rufiventris	Rufous Whistler	20–25		3	
Colluricincla megarhyncha	Little Shrike-thrush	33–38			5
Colluricincla harmonica	Grey Shrike-thrush	52–61		4	
Rhipidura fuliginosa	Grey Fantail	6–8	1		
Rhipidura rufiventris	Northern Fantail	12–14		3	
* **A** *Pomatostomus temporalis*	Grey-crowned Babbler	54–72		3	
** #*Cinclosoma castaneothorax*	Chestnut-breasted Quail-thrush	50–77	1		
Lalage sueurii	White-winged Triller	21–24	1	2,3	
A *Artamus leucorynchus*	White-breasted Woodswallow	40–47		2	
A *Artamus personatus*	Masked Woodswallow	32–36		3	
A *Artamus cinereus*	Black-faced Woodswallow	32–40	1	2	
A *Artamus minor*	Little Woodswallow	15–18		3	
Cracticus nigrogularis	Pied Butcherbird	100–130		3	
** *Anthus novaeseelandiae*	Richard's Pipit	22–26	1		
* **A** *Taeniopygia guttata*	Zebra Finch	11–14	1		
* **A** *Poephila acuticauda*	Long-tailed Finch	13–18		2,3	
* **A** *Poephila personata*	Masked Finch	13–16		2,3	
* **A** *Emblema pictum*	Painted Finch	11–14	1		
* **A** *Erythrura gouldiae*	Gouldian Finch	14–17		3	
Cheramoeca leucosternus	White-backed Swallow	11–15	1		
** ?*Cincloramphus mathewsi*	Rufous Songlark	33–38	1		

+pursued, but not captured (Pettigrew *et al.* 1985).

#listed as *Cinclosoma cinnamomeum* by Douglas (1967); name change due to taxonomic revision.

APPENDIX 2

Avian remains from floor of a *Macroderma gigas* roosting cave at Pine Creek, Northern Territory, collected by S. Hand *et al.* on 10 May, 1983. Abbreviations are: cra, cranium; max, maxilla; man, mandible; ste, sternum; cor, coracoid; sca, scapula; hum, humerus; rad, radius; uln, ulna; car, carpometacarpus; dig, 1st phalanx of 2nd digit; pel, pelvis (s, synsacrum; il, ilium; is, ischium); fem, femur; p, patella; tib, tibiotarsus; f, fibula; tar, tarsometatarsus; pha, phalanx of foot. Figures indicate the number of each element represented in the sample for each taxon.

Taxon	cra	max	man	ste	cor	sca	hum	rad	uln	car	dig	pel	fem	tib	tar	pha
Porzana pusilla/tabuensis Baillon's/Spotless Crake										1						
Turnix castanota Chestnut-backed Button-quail				1	2											
Geopelia striata Peaceful Dove				1								1s				
Geopelia cuneata Peaceful Dove					1							1il/is				
Geopelia cuneata Peaceful Dove				1	2	2	1	1	1	1	1					
Trichoglossus haematodus Rainbow Lorikeet				1	2							1s			1	1
Psitteuteles versicolor Varied Lorikeet					1			1		2						
Apus pacificus Fork-tailed Swift										1						
Alcedo azureus Azure Kingifhser	1	1	1													
Todiramphus sp. kingfisher		1														
Todiramphus ?macleayii Forest? Kingfisher					1											
Philemon argenticeps Silver-crowned Friarbird														1	2	
Meliphagidae (large species) cf. *Philemon argenticeps* (juv) cf. Silver-crowned Friarbird						1								1	1	
Colluricincla harmonica Grey Shrike-thrush										?			1+p	1+f	1	1
Passeriformes (cf. *Artamus* sp.) songbird (cf. woodswallow)															1	
Passeriformes (lark-sized) songbird					1	1										

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